PROC. BIOL. SOC. WASH.
95(4), 1982, pp. 774–780

PARAPROVINCIALISM: REMNANTS OF PALEOPROVINCIAL BOUNDARIES IN RECENT MARINE MOLLUSCAN PROVINCES

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Abstract.—Paraprovincialism is a biogeographical pattern which takes into account Neogene paleoprovincial boundaries that have persisted into the Recent and have been superimposed onto modern provincial arrangements. This pattern is manifested as sets of mutually exclusive, congeneric species pairs that abut along sharply defined boundary lines. An analysis of the paleontology and paleozoogeography of the Caribbean region shows that these Recent species pairs are not true siblings and that their ancestors arose in separate American paleoprovinces; the southern member having a Gatunian ancestor and the northern member having a Caloosahatchian ancestor. Further analysis shows that these Pliocene ancestral pairs were true interprovincial siblings and these are referred to as "ancestromas." The paleozoogeography of the ancestromas is preserved in the Recent by descendant species that have retained the original distributional patterns. Paraprovincialism is found in other provinces, and examples are given for the Recent central South Pacific and Indo-Malayasian regions. In areas where the fossil record is poorly preserved, paraprovincialism may be a useful tool for the reconstruction of Neogene provincial boundaries.

The research that led to the discovery of geographical heterochrony and relict Pliocene molluscan faunas in the Caribbean (Petuch 1981a, b, 1982) has also brought to light a number of other enigmatic biogeographical patterns in that region. One of the most interesting of these is a previously unstudied phenomenon that involves a bipartite distributional pattern within many Caribbean gastropod genera. As is most often the case, the ranges of two congeners are mutually exclusive and will abut along a very well defined boundary line. When found in a province, this pattern occurs in whole suites of species.

Detailed analyses of faunal lists from other molluscan provinces, such as the Indo-Pacific, have also revealed similar patterns for many genera. Since these mutually exclusive species pairs occur too frequently to be simply random events within a single province, I feel that they represent a real biogeographic phenomenon that is here referred to as "paraprovincialism." By using examples of paraprovincialism in the Recent Caribbean gastropod fauna and linking these to the fossil record, I will attempt to explain this problematical pattern of mutually exclusive species pairs and abrupt faunal shifts.

Paraprovincialism in the Caribbean

Malacologists have generally recognized that the Caribbean Molluscan Province can be divided into northern and southern components, each with indicator congeners (Warmke and Abbott 1962:3–21, 319–328; Vermeij 1978:227–236). The

Table 1.—Examples of paraprovincialism in the Caribbean Province.

Restricted to northern Caribbean	Restricted to southern Caribbean
Tegula lividomaculata (C. B. Adams)	*Tegula viridula* (Gmelin)
Astraea americana (Gmelin)	*Astraea tecta* (Lightfoot)
Murex anniae McGinty	*Murex olssoni* E. Vokes
Murex cabritii Bernardi	*Murex donmoorei* Bullis
Murex tryoni Hidalgo	*Murex blakeanus* E. Vokes
Siratus articulatus Reeve	*Siratus springeri* (Bullis)
Dolicholatirus cayohuesonicus (Sowerby)	*Dolicholatirus ernesti* (Van Jutting)
Latirus cariniferus (Lamarck)	*Latirus bernadensis* Bullock
Leucozonia ocellata Gmelin	*Leucozonia lineata* Usticke
Oliva reticularis Lamarck	*Oliva oblonga* Marrat
Olivella mutica (Say)	*Olivella petiolita* (Duclos)
Persicula fluctuata (C. B. Adams)	*Persicula interruptolineata* (Megerle)
Prunum carneum (Storer)	*Prunum prunum* (Gmelin)
Enaeta cylleniformis (Sowerby)	*Enaeta guildingi* (Sowerby)
Conus jaspideus Gmelin	*Conus puncticulatus* Hwass
Conus magellanicus Hwass	*Conus beddomei* Sowerby
Conus spurius atlanticus Clench	*Conus lorenzianus* Dillwyn

ranges of these species pairs, some of which are listed here in Table 1, neatly bisect the Caribbean into separate zoogeographic entities with little faunal overlap. Some zoogeographers, such as Briggs (1974:67–76), further divided the Caribbean into subprovinces based on this bipartite pattern. The boundaries of each subregion were thought to have resulted from ecological differences inherent in insular versus continental components of a single province.

All of these biogeographic schemes, regardless of their bases, delineate faunal changes in approximately the same areas. In the Caribbean Sea, an abrupt shift in species compositions is found along the Honduras-Nicaragua coastline in the west and in the Lesser Antilles in the east (Fig. 1). A classic example is seen in the *Conus jaspideus-C. puncticulatus* species pair (Walls 1979:817–820). The two species coexist on islands from Martinique to the Grenadines, but *C. jaspideus* is the only member found north of this zone and *C. puncticulatus* is the only one to the south.[1] The *Oliva reticularis-O. oblonga* species pair is also a good example, with *O. reticularis* being found only north of the Leeward Islands and *O. oblonga* being found only south of these islands and being most prevalent along northern South America. Along with many other northern members of species-pairs, *Oliva reticularis* and *Conus jaspideus* are always found together in shallow, sandy areas of the northern Caribbean and Greater Antilles. These sympatric species are replaced by *Oliva oblonga* and *Conus puncticulatus* in the same environments in the southern Caribbean.

A review of the paleontological literature of the western Atlantic (references listed at the end of Table 2) showed that each member of a Recent Caribbean species pair descended from a separate ancestral species and not from a single

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[1] The Brazilian variants of "*C. jaspideus*" mentioned by Walls actually are a similar, but different, species that is not related to this particular species-pair. "*Conus jaspideus*" from the islands off northern Venezuela are dwarf *C. mindanus*.

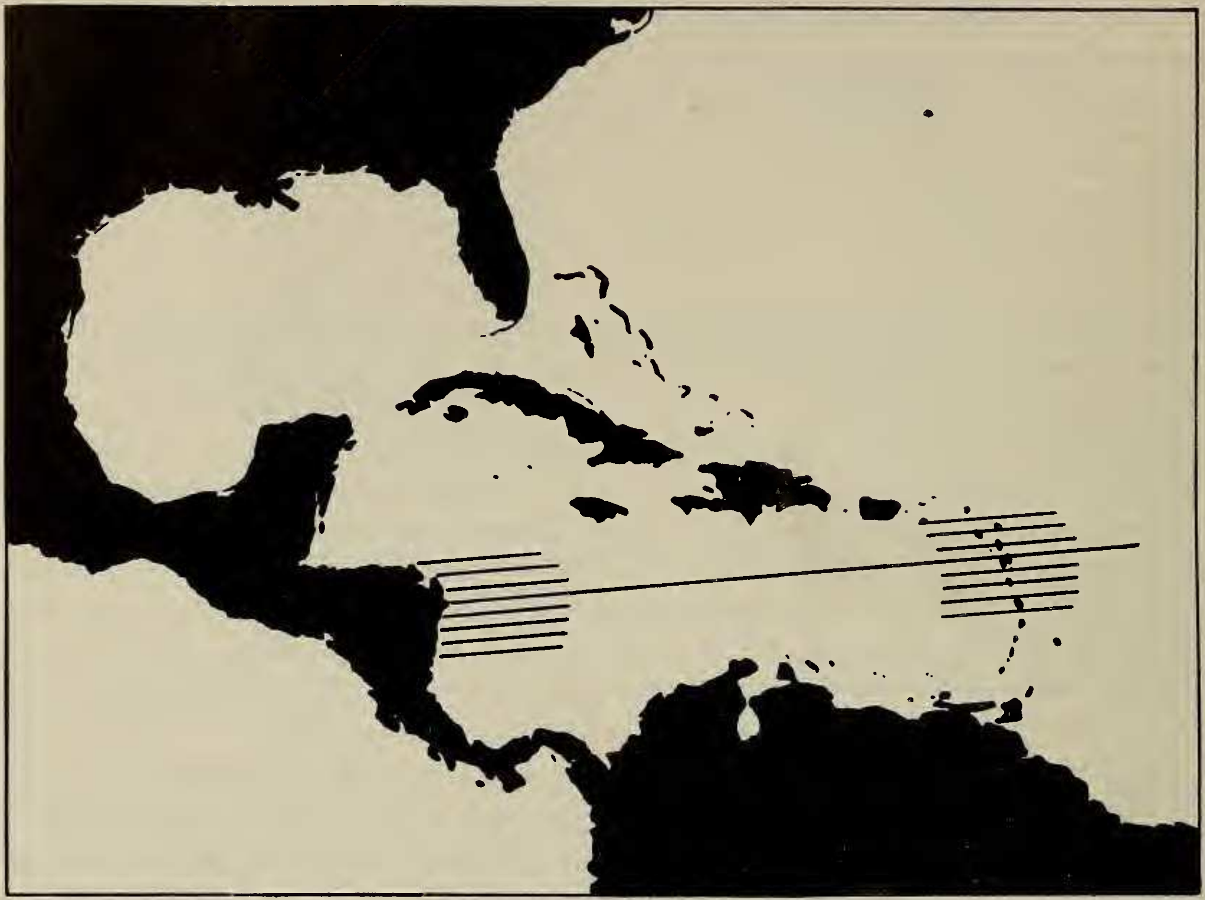

Fig. 1. Map of the Recent Caribbean Sea showing the approximate position of the line of abrupt faunal shift that separates the Caribbean Province into northern and southern components.

common ancestor. Furthermore, many of these separate ancestral forms appear to have been members of their own species pairs in the Pliocene, indicating that the common ancestor for all must date from an earlier time. I will here refer to these ancestral interprovincial sibling species pairs, which were also mutually exclusive in their ranges, as ''ancestromas.'' Some of the Caribbean ancestromas and their living descendant pairs are listed in Table 2. The key to interpreting paraprovincialism, therefore, lies in detecting ancestromas in the fossil record.

For each Caribbean ancestroma that was examined, one member was found to have been restricted to the Gatunian Molluscan Province and one to the Caloosahatchian Molluscan Province (Petuch 1982) (Fig. 2). The Gatunian species gave rise to the Recent southern Caribbean descendant while the Recent northern Caribbean member of the pair arose from the Caloosahatchian member of the ancestroma. The Gatunian and Caloosahatchian Provinces, together, gave rise to the modern Caribbean fauna (Petuch 1982) and it is important to note that their boundaries also ran somewhere along what is now the Nicaragua coastline and the Lesser Antilles.

Paraprovincialism in the Caribbean, then, appears to represent ghosts of precursor paleoprovincial boundaries that have persisted, in secondary form, into the Recent and have been superimposed onto modern zoogeographic patterns. The exact mechanism for the formation of paraprovincialism, however, can only be conjectured at this time. Most probably, the answer will be an ecological one,

Table 2.—Some Recent species pairs and their Pliocene ancestromas. (N) = restricted to Recent northern Caribbean; (S) = restricted to Recent southern Caribbean; (C) = restricted to Caloosahatchian Province; (G) = restricted to Gatunian Province.

Recent pair	Ancestroma
(N) *Astraea americana* (Gmelin)	(C) *Astraea precursor* Dall
(S) *Astraea tecta* (Lightfoot)	(G) *Astraea aora* Woodring
(N) *Murex rubidum* F. C. Baker	(C) *Murex* aff. *recurvirostris* (n. sp.)
(S) *Murex messorius* Sowerby	(G) *Murex polynematicus* Brown
(N) *Latirus cariniferus* (Lamarck)	(C) *Latirus tessellatus* Dall
(S) *Latirus bernadensis* Bullock	(G) *Latirus anapetes* Woodring
(N) *Oliva reticularis* Lamarck	(C) *Oliva carolinensis* Conrad
(S) *Oliva oblonga* Marrat	(G) *Oliva brevispira* Gabb
(N) *Olivella mutica* (Say)	(C) *Olivella dodona* Olsson and Harbison
(S) *Olivella petiolita* (Duclos)	(G) *Olivella venezuelensis* Weisbord
(N) *Enaeta cylleniformis* (Sowerby)	(C) *Enaeta isabellae* (Maury)
(S) *Enaeta guildingi* (Sowerby)	(G) *Enaeta perturbatrix* (Maury)
(N) *Persicula fluctuata* (C. B. Adams)	(C) *Persicula ovula* (Conrad)
(S) *Persicula interruptolineata* (Megerle)	(G) *Persicula mareana* Weisbord
(N) *Prunum carneum* (Storer)	(C) *Prunum onchidella* (Dall)
(S) *Prunum prunum* (Gmelin)	(G) *Prunum macdonaldi* (Olsson)
(N) *Conus jaspideus* Gmelin	(C) *Conus waccamawensis* B. Smith
(S) *Conus puncticulatus* Hwass	(G) *Conus caboblanquensis* Weisbord
(N) *Conus spurius atlanticus* Clench	(C) *Conus cherokus* Olsson and Petit
(S) *Conus lorenzianus* Dillwyn	(G) *Conus longitudinalis* Pilsbry

Ancestromas compiled from Dall 1889, 1890; S. Hoerle and E. Vokes 1978; Jung 1965; Olsson 1922; Olsson and Harbison 1953; Olsson and Petit 1964; Pilsbry 1922; Weisbord 1962; Woodring 1928.

taking into account competitive exclusion at the provincial level. The relationship between paleoprovinciality, ancestromas, and Recent species pairs is shown schematically in Fig. 3.

Predictive Aspects Of Paraprovincialism

Many of the "sibling species" pairs in the Caribbean such as *Oliva reticularis*-*O. oblonga* and *Conus jaspideus*-*C. puncticulatus* are actually pseudosiblings and now can be seen to be separate offshoots of Pliocene ancestromas. For example, these two pairs arose from the Pliocene *Oliva carolinensis*-*O. brevispira* and *Conus waccamawensis*-*C. caboblanquensis* ancestromas, or some other closely related species, and have retained the original distributional patterns of their ancestral species complexes. Altogether, these two and many other Recent gastropod pairs, outline the boundaries of the precursor provinces. In the case of the Caribbean region, with a well-preserved fossil record, reliance on secondary inferences such as paraprovincialism is not necessary for paleoprovincial reconstructions. In areas where the fossil record is poorly preserved, however, paraprovincialism in the modern fauna may be of use to paleontologists in mapping paleoprovincial boundaries.

Many examples of paraprovincialism are also found in the Recent Indo-Pacific

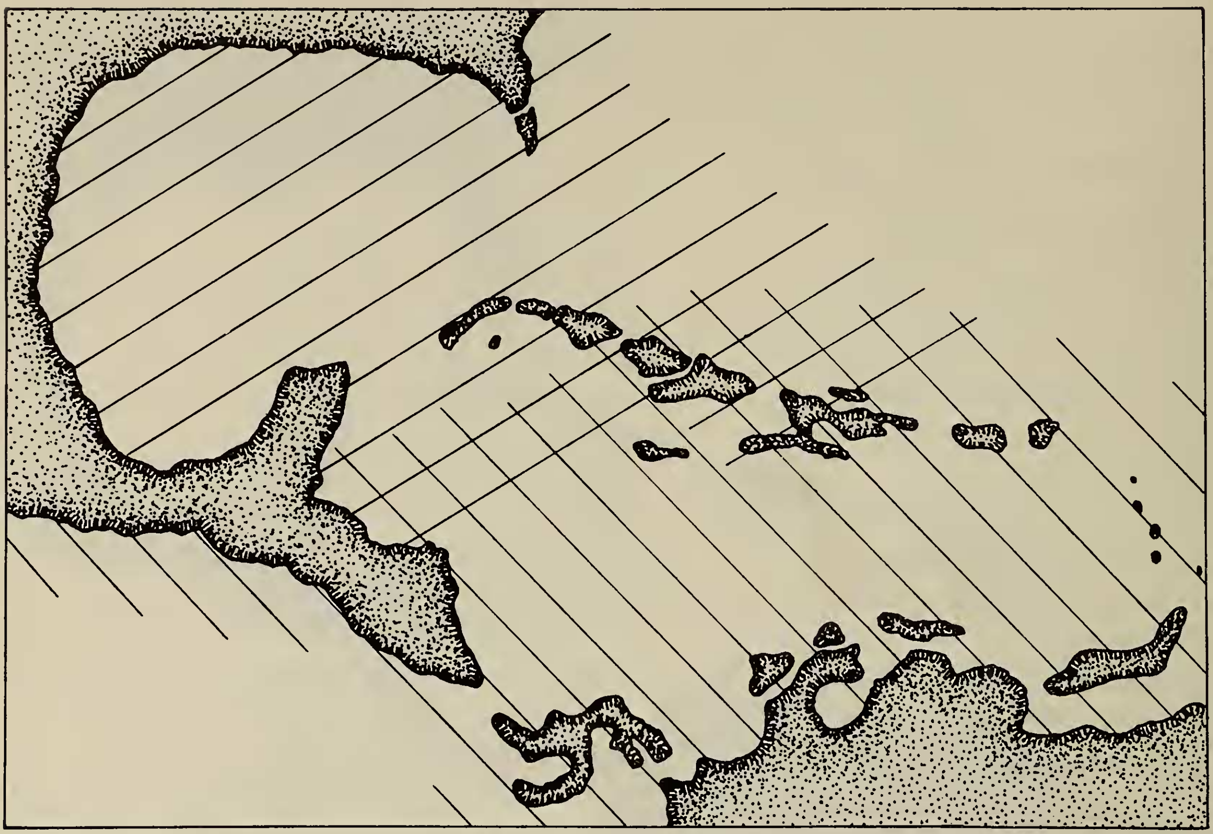

Fig. 2. Map of the Caribbean region in the Pliocene showing the distributions of the Gatunian Province (oblique lines rising to the left) and Caloosahatchian Province (oblique lines rising to the right) (after Petuch 1982).

Molluscan Province. The Cypraeidae are of particular interest here and are useful indicator organisms. In the central South Pacific, a boundary line is sharply delineated, in a north-south direction, from the Phoenix-Canton Atolls to east of Samoa and west of Tonga. To the east of this line are common, wide-ranging species such as *Cypraea serrulifera, C. cumingii,* and *C. obvelata.* To the west of this line are the very similar *C. minoridens, C. catholicorum,* and *C. annulus.* Along this line, no two members of a species pair have ever been found to be sympatric (Burgess 1970).

Many other gastropods follow the same distributional patterns as those of these cypraeids, and their combined ranges may reflect the paleoprovincial distribution of the central South Pacific. Unfortunately, since the fossil record of this area is so poorly known, the existence of ancestromas for most of the species pairs can also only be conjectured at this time. The presence of paraprovincialism, however, implies that the Recent central South Pacific molluscan fauna, like that of the Caribbean, originated from the fusion of two paleoprovinces in the Pleistocene.

The Malaysian Archipelago region of the Indo-Western Pacific also represents an area of faunal shift in a paraprovincial situation. Here, the ranges of such western (Indian Ocean) species as *Strombus decorus, Strombus sibbaldi, Lambis indomaris, Harpa crassa, Oliva ponderosa, Conus maldivus, Conus sumatrensis,* and *Conus fuscatus* abut along those of, respectively, the eastern (Pacific Ocean) "sibling" species *Strombus luhuanus, Strombus plicatus, Lambis scorpio, Harpa*

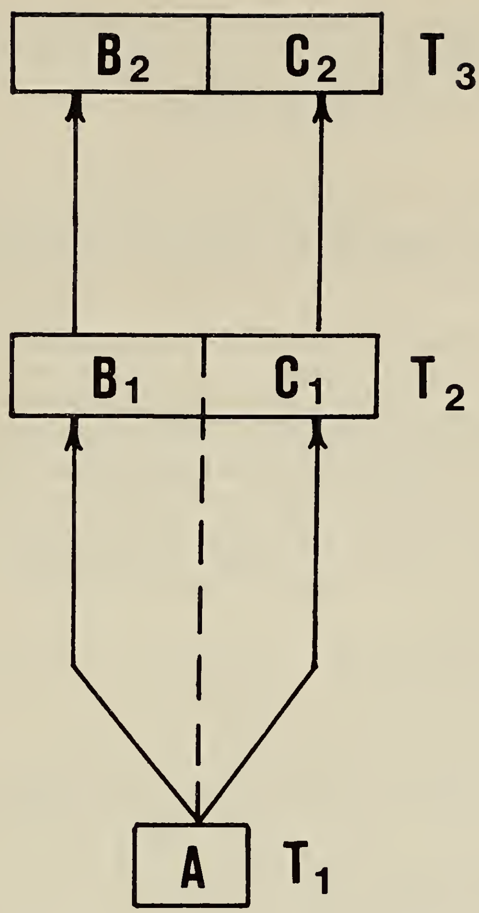

Fig. 3. Schematic diagram of the formation of paraprovincialism in the Recent Caribbean. A = ancestral species at time T_1; B_1, C_1 = components of descendant ancestroma at time T_2 (Pliocene); B_2, C_2 = descendant species pair at time T_3 (Recent). Dashed line between members of ancestroma represents paleoprovincial boundaries; solid line between Recent species pair represents sharp break in distributions.

amouretta, Oliva miniacea, Conus generalis, Conus vexillum, and *Conus imperialis.* These and many other Indian Ocean-Western Pacific species pairs may reflect ancestromas that resulted from provincial differentiation during sea level fluctuations in the Upper Pliocene and Lower Pleistocene.

Judging from the paraprovincialism of the central and western Pacific, it now appears that the Indo-Pacific Molluscan Province, in total, may have resulted from the post-Pleistocene combination of at least three distinct Neogene provinces. As seen in this example and in the previously-mentioned Caribbean region, the search for paraprovincialism in other zoogeographic regions may prove to be a useful tool for the reconstruction of Neogene marine provinciality at the worldwide level.

Acknowledgments

I thank Dr. Geerat J. Vermeij, University of Maryland, and Dr. M. G. Harasewych, University of Delaware, for comments and critical review of the manuscript. Special thanks go to Prof. Arthur J. Cain, University of Liverpool, England, for encouragement and for helping me formulate some of the ideas on paraprovincialism. Thanks also to Mrs. Linda Flanigan for typing the manuscript. The research for this paper was supported by National Science Foundation postdoctoral research fellowship PDF-8166032.

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